

TAXONOMY OF SOME SPECIES OF *PHALLODRILUS*
(OLIGOCHAETA: TUBIFICIDAE) FROM THE
NORTHWEST ATLANTIC, WITH DESCRIPTION
OF FOUR NEW SPECIES

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Abstract.—New material of species of *Phallodrilus* Pierantoni from Georges Bank (SE of Massachusetts), the continental shelf off New Jersey, Maryland, and Virginia, and littoral sediments in Barbados is described. Four of the species, *P. boeschi*, *P. flabellifer*, *P. caviatriatus*, and *P. davis*, are new to science. New taxonomic information is also provided for *P. sabulosus* Erséus, *P. coeloprostatus* Cook, and *P. biprostatus* (Baker and Erséus) n. comb. *Peosidrilus* Baker and Erséus is considered a junior synonym of *Phallodrilus*, as the definition of the latter is modified to include a few species possessing true penes. The relationships between *Phallodrilus* and some other genera within the subfamily Phallodrilinae are discussed.

In 1979 the marine tubificid genus *Phallodrilus* Pierantoni, 1902, was revised by the present author (Erséus 1979a) to include 23 species. Subsequently, several species have been added (Giere 1979; Erséus 1980a, b, 1981a, 1983a, 1984a; Baker 1981; Giani and Martinez-Ansemil 1981), whereas two species have been transferred to other genera (Erséus 1981b, 1982). Thus the genus has comprised no less than 39 species to date. This makes *Phallodrilus* by far the largest genus within the subfamily Phallodrilinae, and yet many species are still undescribed (present paper; Erséus, unpublished). However, *Phallodrilus* is a heterogeneous taxon; for instance, it has hitherto been defined (Erséus 1979a, with slight emendation by Baker 1981) to include both species with and without an alimentary canal. In addition, although the general configuration of the male efferent duct is the same in all the species (vas deferens entering atrium apically or sub-apically, and prostate glands always two per atrium), the terminal part of the duct exhibits considerable variation throughout the genus. In some species the atrium opens directly on the body surface, whereas in others, there are various kinds of pseudopenes developed (with or without copulatory sacs). In some, the "pseudopenial" structure has evolved so far as to approach the situation of a true penis. One such species is *P. minutus* Hrabě, 1973 (see Erséus and Kossmagk-Stephan 1983), another one *P. vanus*, recently described and discussed by Erséus (1984a).

One phallodriline species with a conspicuous (true) penis was regarded as a member of a separate, monotypic genus by Baker and Erséus (1979: *Peosidrilus biprostatus*), despite the fact that the rest of the male duct and the penial setae of that species clearly are *Phallodrilus*-like.

The present paper treats some additional material of *Phallodrilus* from the east coast of the U.S. and from Barbados. Some of the worms represents new species, all exhibiting various degrees of elaboration of the male terminalia in a way which bridges the gap between *Phallodrilus* and *Peosidrilus*. It is therefore proposed here

that *Peosidrilus* becomes a junior synonym of *Phallodrilus*. The paper should, however, be regarded only as a partial revision of the genus; in a forthcoming paper (Erséus, in press), the gutless species of *Phallodrilus* will be scrutinized and taxonomically revised.

Material and Methods

Most of the material used in this study was collected during benthic surveys on the continental shelf off the east coast of the U.S. These projects are (1) the Georges Bank Infauna Monitoring Program, (2) a Bureau of Land Management baseline marine study, and (3) the "Philadelphia Dump Site" study, the latter two made by Virginia Institute of Marine Science off the coasts of New Jersey through Virginia. The specimens were stained with haematoxylin or paracarmine and mounted whole in Canada balsam.

The material of *P. caviatriatus* n. sp. was collected by the author during a stay at the Bellairs Research Institute of McGill University, St. James, Barbados. The worms were fixed in Bouin's fluid; the anterior end of one specimen was subsequently sectioned and stained in Heidenhain's haematoxylin and eosin, whereas the remaining individuals were stained in paracarmine and mounted whole in Canada balsam.

The type-material of the new species has been deposited in the United States National Museum of Natural History (USNM), Washington, D.C.

Phallodrilus sabulosus Erséus, 1979

Phallodrilus sabulosus Erséus, 1979a:188–189, figs. 1–2.—Erséus and Loden 1981: 820–821, fig. 1A.

New material examined.—Two specimens from W of New Jersey, U.S.A., 39°22.1'N, 74°15.6'W, 15.5 m, medium to coarse sand, Aug 1976.

Remarks.—Only one of the new specimens is complete. It is 5.5 mm long and consists of about 45 segments, but its posterior end is not fully developed. Both worms are mature, but pre-copulatory. The penial setae (see Erséus 1979a: figs. 1–2) are one at each side, ventrally in XI; the spermathecal setae (Erséus 1979a: fig. 1) also one at each side, ventrally in X.

This species was previously known only from Florida (Erséus 1979a; Erséus and Loden 1981). Thus the present record considerably extends its known distribution to the north.

Habitat.—Sublittoral, largely coarse sands, known from 3–15.5 m depth.

Distribution.—East coast of the U.S.A., from New Jersey to Florida.

Phallodrilus coeloprostatatus Cook, 1969

Fig. 1

Phallodrilus coeloprostatatus Cook, 1969:16–17, fig. 5.—Brinkhurst and Jamieson 1971:565, fig. 8.38D–F.—Erséus 1979a:189–190, fig. 4.

New material examined.—Four specimens from Georges Bank, SE of Massachusetts, U.S.A., May 1983: two from 40°39.6'N, 67°45.8'W, 78 m; one from 40°39.8'N, 67°46.1'W, 78 m; and one from 40°39.5'N, 67°45.4'W, 78 m; all sites

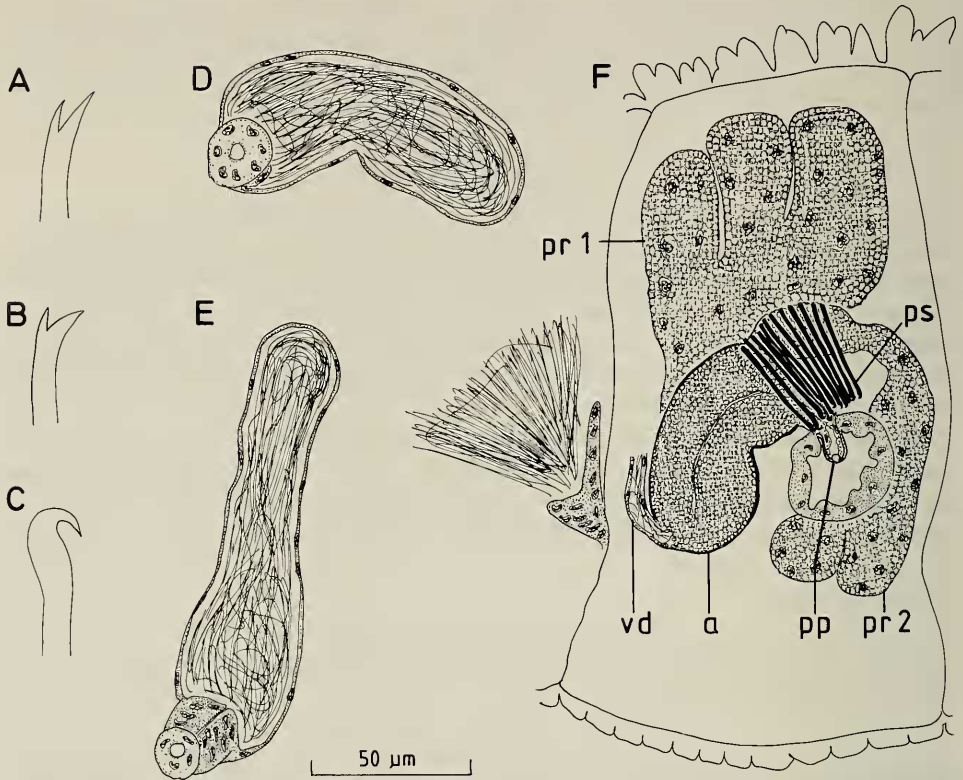


Fig. 1. *Phallodrilus coeloprostatatus*: A, Free-hand drawing of anterior seta; B, Free-hand drawing of posterior seta; C, Free-hand drawing of penial seta; D–E, Spermathecae; F, Lateral view of male duct. a, atrium; pp, pseudopenis; pr 1, anterior prostate gland; pr 2, posterior prostate gland; ps, penial seta; vd, vas deferens.

coarse sand. Four specimens from off Maryland, U.S.A., 38°16'56"N, 74°15'41"W, 28 m, sediment unknown, Apr 1979.

Description of material from Georges Bank.—Length (fixed specimens) 3.6–4.2 mm, 48–54 segments. Diameter at XI, 0.17–0.23 mm. Clitellum extending over X–XI in two of the specimens (see below; location of genital pores), poorly developed in the others. Somatic setae (Fig. 1A–B) bifid, with upper tooth shorter and thinner than lower; teeth slightly more diverging in post-clitellar setae than in anterior setae. Bifids 35–45 μ m long, 1.5–2 μ m thick, 3–4 per bundle anteriorly, (2)3 per bundle in post-clitellar segments. Ventral setae of X (2 specimens), or IX (1 specimen), or VIII (1 specimen) modified into penial bundles (Fig. 1F, ps), each of which contains 9–13 straight, ectally hooked (Fig. 1C) penial setae, 35–40 μ m long, about 1.5 μ m thick. Male pores as small bursae in line with ventral somatic setae, posteriorly in VIII, IX or X. Spermathecal pores in lateral lines in most anterior part of VII, VIII or IX.

Pharyngeal glands poorly visible, but present in V–VI of at least one of the specimens. Male genitalia (Fig. 1F) paired. Vas deferens not observed in full length in available material, but enters atrium more or less apically. Atrium comma-

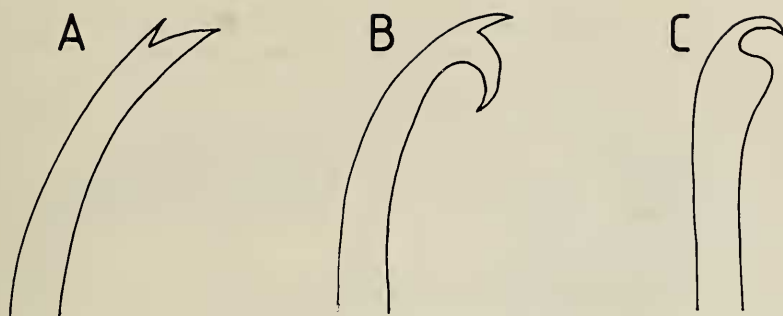


Fig. 2. *Phallodrilus boeschi*, free-hand drawings of setae: A, Anterior seta; B, Posterior, dorsal seta; C, Penial seta.

shaped to almost horseshoe-shaped, about 85 μm long, 25–35 μm wide, with very thin outer lining, and thick, granulated inner epithelium. Anterior prostate gland very large, lobed, attached to ental end of atrium near entrance of vas deferens. Posterior prostate smaller, stalked, attached to ectal part of atrium. Ectal part of atrium abruptly tapering and terminating in small styliform pseudopenial papilla, which protrudes from wall of male bursa. Spermatheca (Fig. 1D–E) 100–150 μm long, 12–37 μm wide, consisting of short ducts and slender, thin-walled ampullae, latter with random masses of sperm.

Remarks.—Morphologically the new specimens from Georges Bank basically conform to the original description of *P. coeloprostatatus* from Cape Cod Bay by Cook (1969), and they are very similar to the specimens of that species reported from off New Jersey by Erséus (1979a). However, the position of the genital organ in the new material is remarkable. In none of the Georges Bank specimens are the spermathecae and male ducts located in segments X–XI as is normal for a tubificid, and as was known for all previously reported individuals of *P. coeloprostatatus*, but they are found in VII–VIII, VIII–IX, or IX–X. This forward shift is even more strongly expressed by the position of the testes (not mentioned in description above): in only one of the four specimens, the testes are located in the spermathecal segment (which is the normal tubificid situation); in all the other worms the testes are located more anteriorly, in the segment next or second next to that bearing the spermathecae.

The four worms from off Maryland exhibit a more moderate tendency towards forward shift of the genitalia; in two individuals the genitalia are in IX–X (with testes in IX), whereas the other two are “normal,” with genitalia in X–XI (testes in X).

It must be concluded here that the specimens with an aberrant location of the genitalia should not be regarded as a separate species, but as variant of *P. coeloprostatatus*. For some reason not yet understood, the otherwise so firmly fixed position of the tubificid genitalia has loosened in some populations of this species. In all other morphological respects, the specimens are identical.

Forward shift of genital organs has been reported for individuals of marine Tubificidae before (e.g., Erséus 1981b, *Giereidrilus inermis*; 1983a, *Bathydrielus sandersi* and *B. argentinae*; Erséus and Davis, 1984, a new species of *Adelodrilus*).

In brief, *P. coeloprostatatus* (sensu lato) can be described as follows: Length 3.6–10 mm, 38–60 segments. Somatic setae, with upper tooth shorter and thinner than lower, 3–5 per bundle anteriorly, (2)3–4 per bundle posteriorly. Penial setae 8–13 per bundle, in fan-shaped formations, and with ectal ends clubbed and hooked (Fig. 1C). Spermathecal pores in lateral lines. Pharyngeal glands extending into VI. Atria more or less horseshoe-shaped, 85–130 μ m long, ending in small, protruding pseudopenial papillae within a pair of shallow male bursae. Prostates very large, lobed.

Habitat.—Sublittoral, largely coarse sands, known from 3.4–78 m depth.

Distribution.—East coast of the U.S.A., from Massachusetts (Cape Cod Bay and Georges Bank) to Maryland.

Phallodrilus boeschi, new species

Figs. 2–3

Holotype.—USNM 96042.

Type-locality.—Off Virginia, U.S.A., 37°06.1'N, 74°33.4'W, 180–200 m, mixed sand, Mar 1976.

Paratypes.—USNM 96043–96046. Four specimens from off Maryland, U.S.A., 38°17.5'N, 74°41.0'W, 29 m, medium to coarse sand, Mar 1976.

Other material examined.—Author's collection: three specimens from the same site as the paratypes; one specimen from off New Jersey, U.S.A., 39°43.6'N, 73°34.8'W, 37 m, medium sand, Mar 1976; and one specimen from Georges Bank, SE of Massachusetts, U.S.A., 40°39.5'N, 67°43.3'W, 72 m, medium to coarse sand, Jul 1982.

Etymology.—The species is named for Dr. D. F. Boesch (now at Lumcon, Chauvin, Louisiana), principal investigator of the Bureau of Land Management baseline study from which most of the material of this species originates, and who first drew my attention to the large collection of marine oligochaetes in the Virginia Institute of Marine Science.

Description.—Length (fixed specimens) 2.8–4.2 mm, 28–39 segments. Diameter at XI, 0.11–0.15 mm. Clitellum extending over $\frac{1}{2}$ X–XIII. Somatic setae (Figs. 2A–B) bifid, 25–45 μ m long, 1–2 μ m thick, 3–5 per bundle anteriorly, 2–3(4) per bundle posteriorly. Bifids with upper tooth much shorter and thinner than lower. Anterior setae (Fig. 2A) with lower tooth straight, almost parallel to upper tooth. Posterior dorsal setae (Fig. 2B) with lower tooth characteristically curved downwards, somewhat prolonged. Setae of mid-body and posterior ventral bundles intermediate. Ventral setae of XI modified into penial bundles (Figs. 3A–B, ps), each of which contains about 10–15 (exact number very difficult to establish) small, straight setae, 20–26 μ m long, maximally 1 μ m thick. Penial setae ectally clubbed, with a strongly bent apical tooth (Fig. 2C). Male pores in line with ventral somatic setae, posterior to middle of XI. Spermathecal pores near lateral lines, in most anterior part of X.

Pharyngeal glands inconspicuous, but extending as far back as into VII or VIII(IX?). Male genitalia (Fig. 3) paired. Vas deferens coiled, 7–9 μ m wide, much longer than atrium. Atrium small, more or less comma-shaped, about 35 μ m long, 12–20 μ m wide, with very thin (up to 1 μ m) muscular lining; ectal part of inner epithelium of atrium granulated, cilia not seen. Prostate glands compact and stalked. Anterior prostate attached with broad stalk to middle of atrium. Posterior

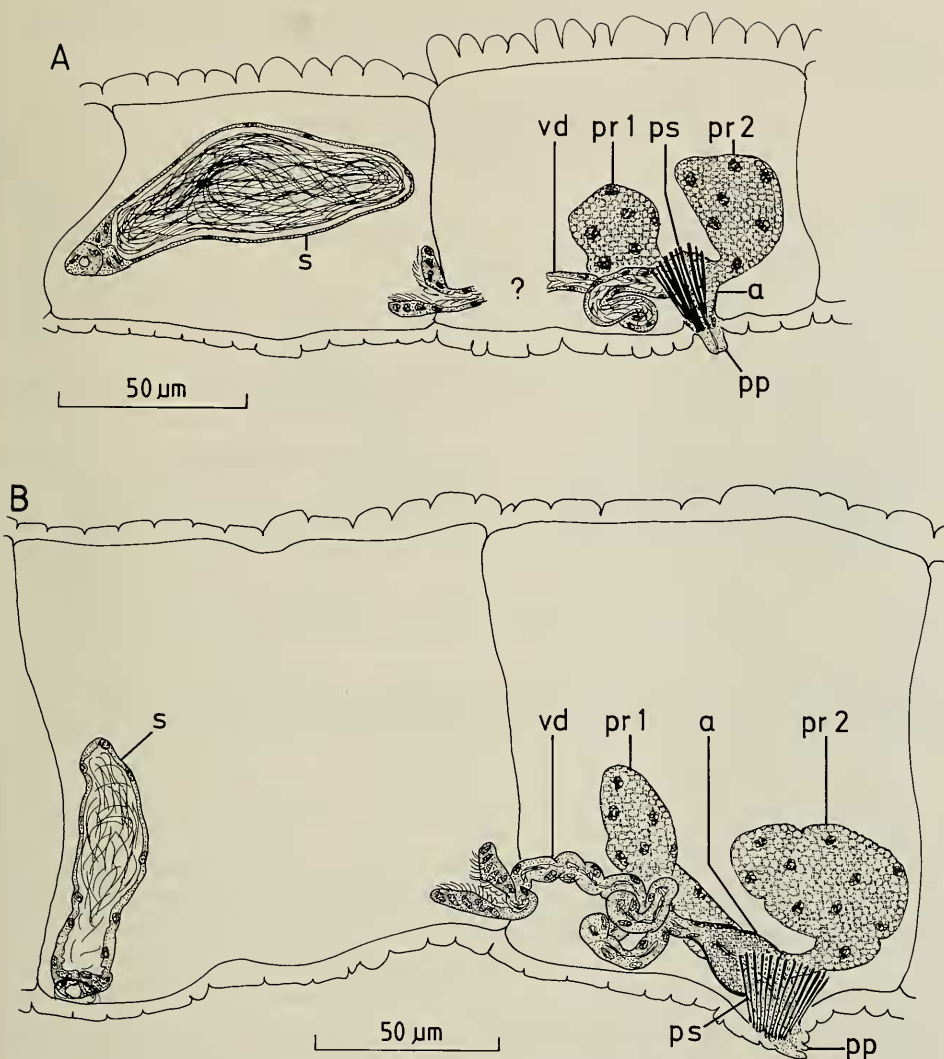


Fig. 3. *Phallodrillus boeschi*, lateral view of spermathecae and male ducts in segments X-XI: A, Specimen from Georges Bank; B, Specimen from off Virginia (holotype). s, spermatheca; other abbreviations as for Fig. 1.

prostate more ectally attached to (posterior face of) atrium. Atrial opening a simple pore lateral to penial setae, but in some specimens ectal end of atrium somewhat protruded to form small pseudopenis (Figs. 3A-B, pp). Spermathecae (Figs. 3A-B, s) 50–65 µm long, maximally 20–30 µm wide, with indistinct and very short ducts, and thin-walled ampullae; latter with random masses of sperm.

Remarks.—This species is closely related and superficially very similar to *P. coeloprostatatus*. However, it is easily distinguished from the latter by the shape of its posterior, dorsal setae (Fig. 2B), and by the small size of its atria; length only about 35 µm as opposed to 85–130 µm for *P. coeloprostatatus*.

Habitat.—Sublittoral, medium to coarse sand, known from 29–200 m depth.

Distribution.—East coast of the U.S.A., from Massachusetts (Georges Bank) to Virginia.

Phallodrilus flabellifer, new species

Fig. 4

Holotype.—USNM 96047.

Type-locality.—Georges Bank, SE of Massachusetts, U.S.A., 40°39.6'N, 67°45.8'W, 78 m, coarse sand, May 1983.

Paratypes.—USNM 96048–96049. Two specimens from Georges Bank: one from 40°39.5'N, 67°46.2'W, 79 m, medium to coarse sand, May 1983; and one from 40°39.5'N, 67°45.4'W, 78 m, coarse sand, May 1983.

Other material examined.—Author's collection: one specimen from the type-locality.

Etymology.—The name *flabellifer* (Latin for “fan-bearing”) alludes to the fan-shaped arrangement of the penial setae of this species.

Description.—Length (fixed, complete specimens) 3.0–3.3 mm, 29–34 segments; one specimen, which is not complete but very stretched, is 4.5 mm long, but still only consisting of first 28 segments. Diameter at XI, 0.11–0.16 mm. Clitellum extending over XI and at least anterior half of XII, but poorly developed in available specimens. Somatic setae (Fig. 4A) bifid, with upper tooth thinner and slightly shorter than lower. Bifids 35–45 μ m long, 1–1.5 μ m thick, 2 per bundle throughout body. Ventral setae of XI modified into penial bundles (Fig. 4C, ps), each of which containing 13–15 straight, ectally hooked (Fig. 4B) setae, arranged in fan-shaped formation. Penials 30–37 μ m long, about 1.5 μ m thick. Male pores in line with ventral setae posteriorly in XI. Spermathecal pores in line with ventral setae in most anterior part of X.

Pharyngeal glands in III–IV(V), poorly developed. Male genitalia (Fig. 4C) paired. Vas deferens about 5 μ m wide, thin-walled and very long, entering apical end of atrium. Atrium somewhat spindle-shaped, only slightly curved, 60–80 μ m long, 17–25 μ m wide, with 1–2 μ m thick outer lining of muscles, and inner granulated and ciliated epithelium. Lumen of atrium wide. Prostate glands moderately large, anterior one attached to apical end of atrium, near entrance of vas deferens, posterior one to ectal end of atrium. Atrium opening directly on body surface immediately anterior to ectal ends of penial setae. Spermathecae with distinct ducts, 35–50 μ m long, 11–14 μ m wide, and thin-walled ampullae, 70–120 μ m long, 23–35 μ m wide; latter with loose and random sperm.

Remarks.—The fan-shaped penial bundles of *P. flabellifer* are reminiscent of those of *P. coeloprostatatus* and *P. boeschi*, but the new species differs from the others in two important respects: (1) its somatic setae are arranged in bisetal bundles throughout the body, whereas most bundles of *P. coeloprostatatus* and *P. boeschi* each contain 3, 4 or 5 setae; and (2) its atria are spindle-shaped and hollow (lumen and ciliation easily seen), whereas the atria are of other shapes and with very narrow lumens in the other two species.

Phallodrilus obscurus Cook, 1969, which was redescribed on the basis of fully mature specimens by Erséus (1980a), is possibly also a close relative of *P. flabellifer*. That species, however, has a very high number of somatic setae (up to 7

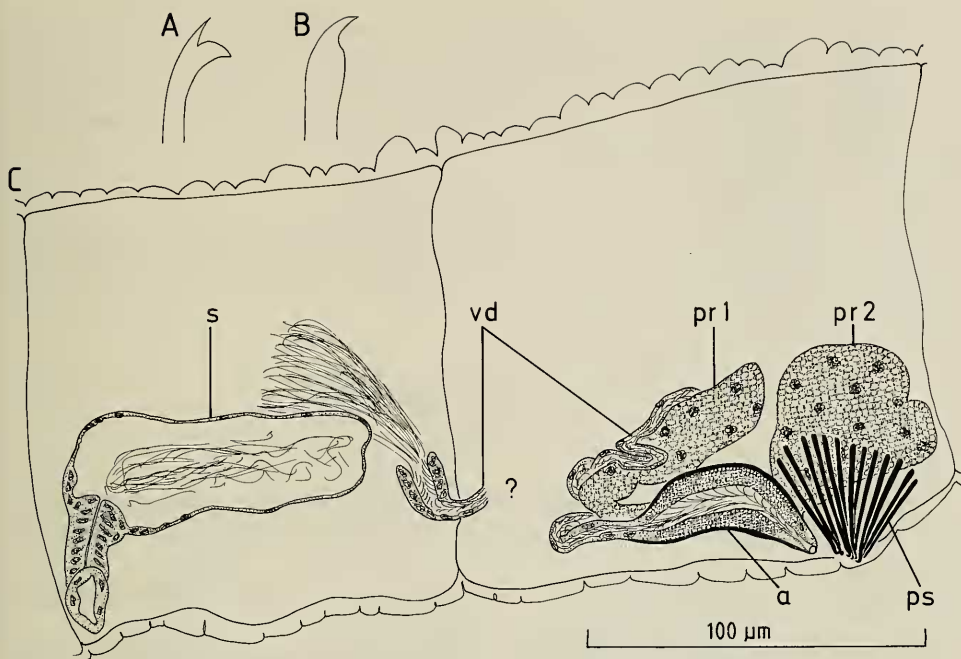


Fig. 4. *Phallodrilus flabellifer*. A, Free-hand drawing of somatic seta; B, Free-hand drawing of penial seta; C, Lateral view of spermatheca and male duct in segments X–XI. Abbreviations as for Fig. 3.

per bundle anteriorly) and its penial setae are more or less parallel within the bundles, not arranged in a fan as in *P. flabellifer*.

Habitat.—Sublittoral, largely coarse sand, known from 78–79 m depth.

Distribution.—Known only from Georges Bank, SE of Massachusetts.

Phallodrilus biprostatatus (Baker and Erséus, 1979), new combination

Peosidrilus biprostatatus Baker and Erséus, 1979:506–508, figs. 1–2 [Note that due to a typographical error the legend of fig. 2 was deleted from a part of the circulation of this publication. It should read: “Fig. 2. *Peosidrilus biprostatatus*: Lateral view of spermatheca and male genitalia in segments X and XI. Abbreviations: a, atrium; p, penis; pr 1 and pr 2, prostate glands; psa, penial sac; pse, penial setae; s, spermatheca; vd, vas deferens.”].—Erséus and Loden 1981: 819–820.

Remarks.—This species was described from sublittoral sediments off New Jersey and North Carolina (Erséus and Baker 1979), and subsequently reported from a similar habitat off the E coast of Florida (Erséus and Loden 1981).

The species is characterized by a pair of large penes with bulbous bases, separated from the atria proper by constrictions, and *P. biprostatatus* was, because of this striking feature, assigned to a monotypic genus, *Peosidrilus* Baker and Erséus, 1979. However, in other important characters, such as the penial setae (apically

clubbed and hooked), atria and prostate glands, the species is very similar to most of the *Phallodrilus* species treated in the present paper. It is now concluded that the penis of *Peosidrilus biprostatus* is just an elaboration of the pseudopenial structure found in several *Phallodrilus* forms, and consequently, the species is here transferred to the latter genus.

Habitat.—Sublittoral, medium to very coarse sands, known from 5.5–73 m depth

Distribution.—East coast of the U.S.A., so far recorded from New Jersey to Florida, but the species has recently been found on Georges Bank, SE of Massachusetts (Mr. D. Davis, pers. comm.).

Phallodrilus caviatriatus, new species

Fig. 5

Holotype.—USNM 96050.

Type-locality.—River Bay, NE Barbados, West Indies, inner end of bay at mouth of a stream, low water mark, coarse sand, probably often subject to brackish-water conditions; 27 Oct 1979.

Paratypes.—USNM 96051–96052. One sectioned and one whole-mounted specimen from the type-locality.

Other material examined.—Author's collection: one specimen from the type-locality.

Etymology.—The name *caviatriatus* refers to the hollow (=Latin “cavus”) nature of the atrium of this species.

Description.—Length (fixed specimens) 3.9–4.6 mm, 40–45 segments. Diameter at XI, 0.23–0.29 mm. Clitellum extending over $\frac{1}{2}$ X– $\frac{3}{4}$ XII in whole-mounted paratype, poorly developed in other specimens. Somatic setae (Fig. 5A) bifid, with upper tooth thinner and slightly shorter than lower, and often with thin ligament connecting tip of lower tooth with setae shaft. Bifids 35–50 μ m long, 1.5–2.5 μ m thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments (occasionally “bundles” unisetal, or missing). Ventral setae of XI modified into penial bundles (Fig. 5D, ps), each of which containing about 13–18 (exact number often difficult to establish) straight, ectally clubbed setae, 40–55 μ m long, about 2 μ m thick. Ectal “clubs” of penials bearing a strongly curved apical tooth, but only seen in side view (see Fig. 5B). Penial setae located immediately ventral to male openings, at bases of penes. Male pores in line with ventral setae, posteriorly in XI. Spermathecal pores slightly dorsal to line of ventral setae, in most anterior part of X.

Pharyngeal glands extending into V, and most anterior part of VI. Male genitalia (Fig. 5C–D) paired. Vas deferens 9–12 μ m wide, slightly shorter than atrium, entering apical, ental end of atrium. Atrium cylindrical, hollow, characteristically bent at middle, with conspicuous circular muscles, 5–9 μ m thick, and ciliated inner epithelium; epithelium much thinner in ental part than in ectal part of atrium; atrium about 150–200 μ m long (exact length difficult to establish), ental part 45–60 μ m wide, ectal part 30–35 μ m wide; ectal part tapering into slender duct leading to wedge-shaped, rounded penis (cf. Fig. 5C). Two compact, small prostate glands present, one at entrance of vas deferens, another located posterior to, and attached to, atrial duct; stalks of prostates not well developed. Sperma-

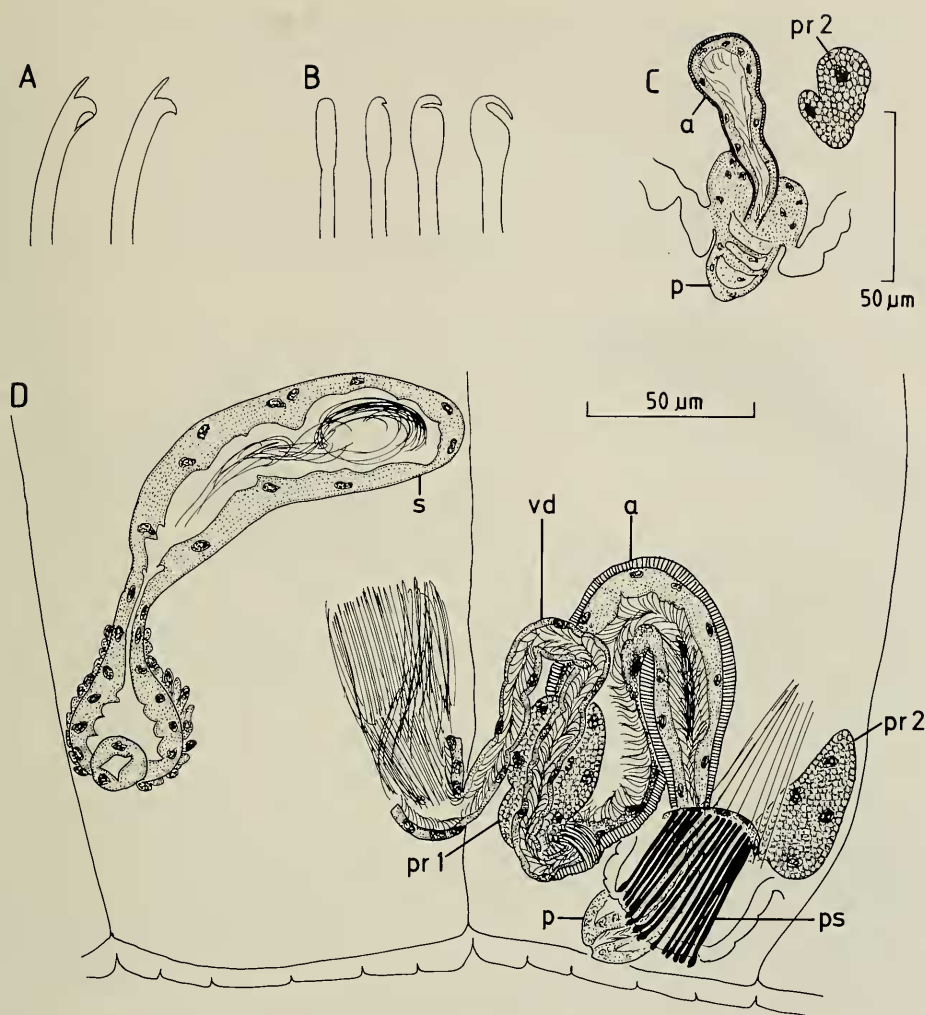


Fig. 5. *Phallodrilus caviatriatus*: A, Free-hand drawings of somatic setae; B, Free-hand drawings of penial setae, as seen from different angles; C, Section through terminal part of atrium and penis; D, Lateral view of spermatheca and male duct in segments X-XI. p, penis; other abbreviations as for Fig. 3.

thecae (Fig. 5D, s) slender, consisting of 80–90 μm long ducts, and 70–115 μm long, 40–45 μm wide ampullae; ducts with bulbous outer portion, 30–45 μm wide, and narrow inner portion, only about 10–12 μm wide; ducts gradually widening into ampulla, having thick walls and containing random sperm.

Remarks.—The hollow ental half of the atrium is the most striking feature of *P. caviatriatus*, and it clearly distinguishes the species from other *Phallodrilus*. The penes are similar to, but not quite as pendant and deeply located within the penial sacs as, those of *P. biprostatus*.

Habitat.—Intertidal coarse sand.

Distribution.—Known only from the type-locality in Barbados.

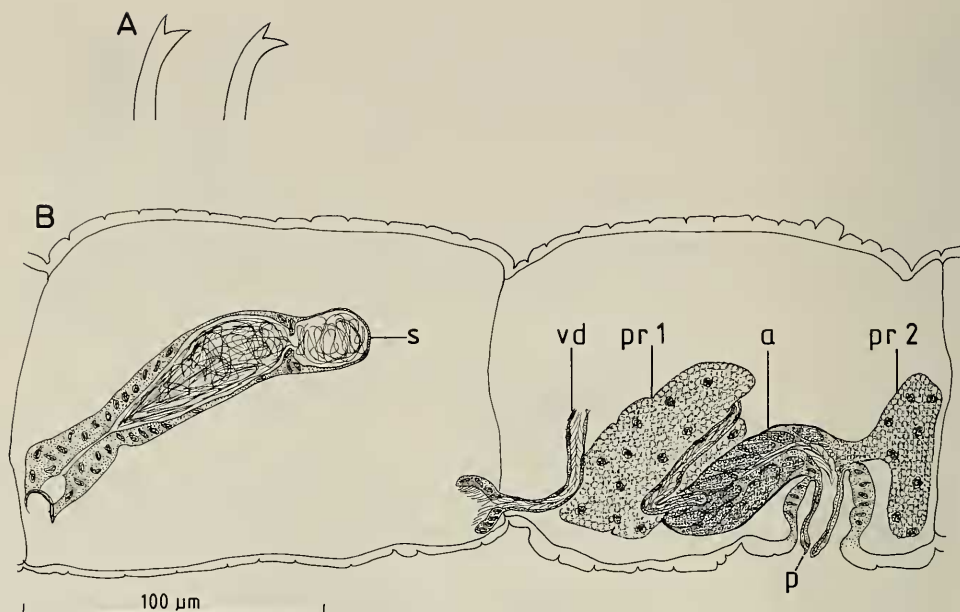


Fig. 6. *Phallodrilus davis*: A, Free-hand drawings of setae; B, Lateral view of spermatheca and male duct in segments X–XI. Abbreviations as for Fig. 5.

Phallodrilus davis, new species

Fig. 6

Holotype.—USNM 96053.

Type-locality.—Georges Bank, SE of Massachusetts, U.S.A., 40°39.6'N, 67°45.8'W, 78 m, coarse sand, May 1983.

Paratypes.—USNM 96054–96055. Two specimens from Georges Bank: one from 40°39.5'N, 67°46.5'W, 79 m, coarse sand, May 1983; and one from 40°39.4'N, 67°46.9'W, 80 m, medium to coarse sand, May 1983.

Other material examined.—Author's collection: one specimen from 40°39.3'W, 67°46.2'W, 79 m, medium to coarse sand, May 1983.

Etymology.—This species is named for Mr. Dale Davis (Battelle New England Marine Research Laboratory), who very kindly provided the material of *Phallodrilus* from Georges Bank.

Description.—Length (fixed specimens) 3.4–4.4 mm, 36–41 segments. Diameter at XI, 0.12–0.18 mm. Clitellum extending over at least XI– $\frac{1}{2}$ XII (not fully developed in some specimens). Setae (Fig. 6A) bifid, with upper tooth thinner and shorter than lower. Setae 40–70 μm long, 1.5–2.5 μm thick, (2)3–4 per bundle throughout body except for ventral bundles of XI, which are absent. Male pores in line with ventral setae in posterior part of XI. Spermathecal pores in line with ventral setae in most anterior part of X.

Pharyngeal glands in III–IV, but poorly developed. Male genitalia (Fig. 6B) paired. Vas deferens about 4–5 μm wide, long and thin-walled, entering atrium subapically. Atrium sigmoid- to comma-shaped, 65–85 μm long, 21–32 μm wide, with very thin outer lining of muscles and thick inner granulated and (at least

partly) ciliated epithelium; granulation of atrium confined to drop-shaped aggregations (each one an epithelial cell?). Anterior prostate gland large, attached to apical end of atrium. Posterior prostate smaller than anterior one, stalked and attached to most ectal end of atrium. Atrium terminating in cylindrical, ectally somewhat pointed penis, latter pendant within penial sac. Penis 25–30 μm long, 6–12 μm wide at middle, hollow, and appearing stiff, but cuticular lining not thickened into sheath. Spermathecae (Fig. 6B, s) slender, about 125 μm long, maximally 25–40 μm wide, consisting of ectal ducts, gradually widening into thin-walled ampullae; lumen of latter often incised at one or more places; sperm as random masses.

Remarks.—*Phallodrilus davis*i is the only known species of *Phallodrilus* which combines the possession of true, pendant penes with the lack of penial setae.

Habitat.—Sublittoral, largely coarse sands, known from 78–80 m depth.

Distribution.—Known only from Georges Bank, SE of Massachusetts.

Modified Definition of the Genus *Phallodrilus* Pierantoni, 1902

Diverse group of predominantly marine tubificids. Hair setae absent. Penial setae generally present. Spermathecal setae occasionally present. Male and spermathecal pores paired, generally in segment XI and X, respectively (exceptions, see *P. coeloprostat*us above, and *P. postspemathecatus* Erséus, 1980b). Coelomocytes, if present, small and sparse, not of the “rhyacodriline-type.”

Male efferent ducts paired. Vasa deferentia ciliated, not dilated and storing sperm, but (generally) narrow and clearly set off from atria. Vasa deferentia join apical or subapical, ental ends, but never ectal halves of atria. In some species copulatory structures present, as protrusible pseudopenes or non-cuticularized true penes. Two pairs of prostate glands present; the anterior pair always attached to atria near entrances of vasa deferentia, posterior pair generally attached to ectal ends of atria; prostates often stalked. Spermathecae paired, generally longer than wide. Sperm in loose masses or bundles in spermathecae; spermatozeugmata and external spermatophores absent.

Type-species.—*Phallodrilus parthenopa*eus Pierantoni, 1902.

Discussion

The definition of the genus *Phallodrilus* provided above has been modified to include some species with true penes (*biprostatus*, *caviatriatus* and *davis*i; all treated in the present paper). It excludes, however, some other phallodriline species with penes, such as the members of the genera *Aktedrilus* Knöllner, 1935, and *Bacescuella* Hrabě, 1973 (see Baker and Erséus 1982; Erséus 1978, 1980c, 1984a–c; Erséus and Kossmagk-Stephan 1982; Finogenova and Shurova 1980; Hrabě 1973; Strehlow 1982). In these genera the spermathecae, when present, are unpaired, middorsal, and the penes are certainly not homologous to those of the three *Phallodrilus* species mentioned above. In addition, in *Bacescuella* sperm are transferred by means of external spermatophores, a mode not known for any other genus within the Phallodrilinae.

In the previous definition (Erséus 1979a), it was stated: “alimentary canal absent in some species.” This sentence is now deleted, as the gutless species of *Phallodrilus* will be removed from that genus in a separate revision (Erséus, in press).

A great taxonomic problem with *Phallodrilus* is that the male efferent ducts of most of its species conform to a basic phallodriline plan, from which the male ducts of most other genera within the subfamily can be derived. This means that *Phallodrilus*, as defined here and previously, is a paraphyletic rather than a strictly monophyletic taxon (a "paraphyletic" group does have and includes a common ancestor, but it does not include all the descendants of that ancestor). Unfortunately, there does not seem to be any way out of this dilemma. A widening of *Phallodrilus* to a level where one would be confident that it was a strictly monophyletic group would imply that virtually all of the 15 phallodriline genera were united to form one large genus, which would hardly be beneficial for the classification of the very diverse subfamily Phallodrilinae. On the other hand, a splitting of today's *Phallodrilus* into smaller, monophyletic genera is, at present at least, impossible. One can of course recognize several species groups within *Phallodrilus*, which within themselves are monophyletic and can be defined on the basis of their synapomorphies, but if all these groups were raised to the level of genera, the remaining species would just become a large, most probably polyphyletic group, defined only by its plesiomorphic characters.

It is, therefore, considered appropriate to accept that *Phallodrilus* remains paraphyletic, but to define it in a way which allows for some short lineages of derived species; *P. biprostatus*, *P. caviatriatus* and *P. davis* are examples of such derived species. It is a much different situation with large, coherent groups, such as *Aktedrilus* (references given above) and *Adelodrilus* Cook, 1969 (see Erséus 1983b; Erséus and Davis, 1984). *Aktedrilus* now contains 16 species, *Adelodrilus* 14, and they are both easily recognized and classified as genera on the basis of their shared derived characters (synapomorphies) (*Aktedrilus*: unpaired dorsal spermatheca, well developed penes, lack of penial setae, and littoral habitat; *Adelodrilus*: dilated vasa deferentia storing sperm, and highly modified penial setae).

Most of the *Phallodrilus* species treated in the present account, viz. *P. coeloprostat*, *P. boeschi*, *P. flabellifer*, *P. biprostatus*, and *P. caviatriatus*, share the feature of small, multiple penial setae with characteristically clubbed and apically hooked tips (Figs. 1C, 2C, 4B, 5B; Baker and Erséus 1979, fig. 1C). It is noteworthy that these are all northwest Atlantic species and that there are no other known *Phallodrilus* with this kind of penial setae in other areas of the world. It seems feasible to regard these species as a monophyletic group within the genus and that it has evolved and radiated in the northwest Atlantic.

This group, however, is not the only one within the Phallodrilinae with the "clubbed and hooked" penial setae. Such setae are characteristic also for most species within *Adelodrilus* (see Erséus 1983b) and the monotypic *Bermudrilus* Erséus, 1979 (see Erséus 1979b). The geographical records of the latter genera are largely confined to the East coast of the U.S.; one species is known also from Bermuda and a few species are described from Europe (Erséus 1983b). It should be noted that the knowledge of marine Tubificiade from the northwest Atlantic is perhaps better than that from any other part of the world, but if *Adelodrilus* and *Bermudrilus* were present in, for instance, the Pacific Ocean, one would have expected these genera to turn up in the fairly extensive collections that now have been made there (the work by H. R. Baker in British Columbia; Erséus 1981a, 1984a, and unpublished). It therefore appears likely that the *Adelodrilus-Bermudrilus* lineage originated in the first area, or at least within a fauna the de-

scendants of which today inhabit this region. This would imply that the *Adelodrilus-Bermudrilus* assemblage split off relatively late from their ancestral stock within (most probably) *Phallodrilus*, a stock probably closely related to the Recent group of *Phallodrilus* treated in the present paper. The high number of closely related species of *Adelodrilus* within one restricted area (the U.S. east coast continental shelf; Erséus 1983b, Erséus and Davis, 1984) demonstrates how successful and radiative speciation has been within this particular group.

Acknowledgments

Specimens from Georges Bank were collected as part of the Georges Bank Benthic Infauna Monitoring Program, supported by contract number 14-12-0001-2912 from the U.S. Department of the Interior Minerals Management Service to Battelle New England Marine Research Laboratory.

I am much indebted to Dr. D. F. Boesch, Dr. R. J. Diaz (Virginia Institute of Marine Science), and Mr. D. Davis, for providing the oligochaete material and important information; Mr. Davis also kindly read and commented upon the first draft of the manuscript; to Dr. F. Sander (former director of Bellairs Research Institute of McGill University), for working facilities in Barbados; to Mrs. Barbro Löfnertz, for skilful technical assistance; and to the Swedish Natural Science Research Council, for financial support.

This paper is a contribution from the Bellairs Research Institute of McGill University, Barbados.

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